

General Relativistic Biology

May 17, 2015

Abstract

This paper presents an alternative conceptual foundation for biological evolution. First the causal and statistical perspectives on evolutionary fitness are analyzed, finding them to implicitly depend on each other, and hence cannot be individually fundamental. It is argued that this is an instance of a relativistic perspective over evolutionary phenomena. New accounts of fitness, the struggle for life, and Natural Selection are developed under this interpretation. This biological relativism is unique in that it draws from General Relativity in physics, unlike previous theories that drew upon statistical mechanics or Newtonian dynamics. A mathematical law of evolutionary change, as well as new theoretical biological concepts to underpin it, are likewise developed. The law and theory are then applied to give examples

of how both cornerstones and edge cases can be understood using these new methods. Using General Relativistic Biology provides fresh insight into evolution, all while preserving the core, canonical scientific research program.

1 Introduction

This paper presents an alternative conceptual foundation for biological evolution. I start by discussing the problem posed by the causal and statistical interpretations of fitness. Though the two camps appear diametrically opposed, it is argued that both implicitly rely upon the other. To find middle ground the causal and statistical interpretations of fitness are recast as relativistic perspectives of a single fundamental fitness property. This new concept of relativistic fitness will then be developed into a general theory of evolution by drawing on General Relativity from physics.

At first blush this theory could be seen as following in the historical footsteps of physics: just as Newtonian Gravity gave way to Einstein's General Relativity, so too will the Newtonian model of Natural Selection give way to a relativistic model. While I invite this comparison, mere historical similarity will neither provide the foundation nor philosophical sophistication required for a theory meant to be a serious alternative to Darwinian evolution.

Therefore, after appropriating the methods and framework of physics, examples and implementations that follow from the new biological theory will be given to demonstrate its conceptual mileage for philosophy of biology, theoretic biology and, potentially, practical scientific application. Besides showing the range and depth of the theory, it also serves to provide food for biological thought. This utility in solving problems and stimulating new ways to think about evolution lends plausibility to describing biological evolution in these relativistic terms.

By tracing from conceptual foundations to practical results, the strategy is to create a new unified picture, a paradigm that provides an understanding of evolution that preserves and expands upon the successes of Darwinism.

2 Evolution and Causality

The fundamental explanatory scheme of biological evolution uses the concept of fitness to understand Natural Selection. Over the last decade or so there's been a debate centered over the causal status of biological fitness. Let us grant each of the two main camps, the statisticalists, such as Matthen and Ariew (2002) and Walsh et al. (2002), and the causalists, such as Stephen (2004) and Northcott (2010), their own version of fitness: Statistical Fitness and Causal Fitness. What are these two

fitnesses? According to (Walsh, 2010, 147-8), Causal “Fitness is (or measures) the propensity of a trait type to change in relative frequency in a population. . . . Natural selection, it seems to follow, is a population-level causal process; it is that process caused, and measured, by fitness distribution.” Statistical “fitness is a mere statistical, noncausal property of trait type. . . . Fitness distribution explains but does not cause the changes in a population undergoing natural selection.”

Put more prosaically, Causal Fitness is competitive: a more fit organism will outcompete a less fit one, on average, as a causal result of their traits. It is compared Newtonian Gravity in that it is a fundamental force that causes change. Just as the gravity of a mass has an effect on the motion of another mass, the fitness of one population will have a biological effect on other populations.

Statistical fitness, on the other hand, describes the environmental situation: fitness is statistically correlated with changes in the environment, but does not cause them. This is compared to Statistical Mechanics in that it acts like a gas. A gas, if otherwise not acted upon, will reach some average temperature, even if one part was originally warmer. The distribution of heat is not due to some causal process of the gas, but of the underlying motion of the particles. Similarly a population organisms may distribute itself through an environment, but this is due to the underlying physical properties of that system and not some causal property

of the population.

Without a reconciliation between these causally opposed viewpoints, we have a fundamental disagreement over how we understand the basic scientific concepts of evolutionary biology.

2.1 The Hard Problem of Evolution

Though each claims to be the ultimate measure, as Ramsey (2013) and Hitchcock and Velasco (2014) recently note, this research into fitness has not yielded agreement and the arguments often go past each other (Ramsey, 2013, 10). Moreover, while each position solves certain questions within evolution, neither gets at the underlying hard causal problem. Lets first take a look at the Causalist position:

The Causalists hold that Natural Selection causes evolutionary change, but is independent of the underlying physics. The question is how does this change occur, since Natural Selection is a non-physical force? It would have to be a non-physical force causing some physical result. This is problematic because even if we can't currently describe the entire physical reality with physics, any given small-scale phenomenon can be adequately explained with a physical cause. So, without a connection between biological and physical causality, given no environmental-level Cartesian pineal gland, there is no way for Natural Selec-

tion to have noticeable physical consequences. Hence, since Natural Selection is fundamental for the Causalists, there is no effective causal structure.

On the other hand, Statisticalists describe Natural Selection as shorthand for the underlying causal physics. Since we can't describe physics to sufficient complexity, we use Natural Selection as a heuristic. However if Natural Selection were just a heuristic, then it should only work under a limited scope and fail when it is applied otherwise. Like any other heuristic or shorthand, it should work very well but only in a few cases. On the contrary, the use of evolutionary concepts is only growing and being extended across many different fields, such as computer science, psychology and linguistics. Natural Selection has proven to be a robust concept, much more than a mere convenience. Therefore the Statisticalist, in treating Natural Selection as a heuristic, has oversimplified the phenomenon by failing to capture its depth.

Given these difficulties neither side can claim fundamentality. The Causalists fail without the physical interaction, and the Statisticalists fail without the biological sophistication. Since the ontological gap between biology and physics is yet too great, we are left with a dualistic understanding of Natural Selection.

2.2 Bridging Statistical and Causal Fitness

What has been missed is that the distinction between Statistical Fitness and Causal Fitness cannot be maintained universally. The debate, as described below, has been over two sides of the same coin.

First note that the two views do not differ in their results, in spite of their different explanatory schemes. Given some biological adaptation, both causal or statistical explanations will conclude with the adaptation having a qualitatively similar fitness. That is, while the measurements and explanations may be conventions of their respective systems, the qualitative conclusion of high or low fitness is common to both theories. A causally high fitness for some organisms will always correspond to a statistically high fitness for those organisms, and vice versa. These results hint at some deeper connection, but this is not represented by either viewpoint.

Second, let's discuss causal and statistical descriptions of fitness. Take a causal biological story: assume that a mistletoe plant (or population of mistletoe) has an adaptation that makes it more competitively fit. The adaptation could be for any trait, but let's say the trait is that its berries taste better to birds that distribute seeds.

These tastier berries are a biological adaptation and, by definition, are the re-

sult of genetic mutations. But where did the mutation come from? Mutations are caused by environmental factors, such as errors in copying genetic material—a factor of the cellular environment—or by UV or nuclear radiation. Hence, although this is a causal story, it begins with a non-biologically-causal statistical anomaly. Insofar as all causal stories rely on mutations at their start, all causal fitness is dependent upon the background environmental situation.

Now let's look at a statistical biological story. Again take the two different organisms (or populations) of mistletoe, and one with tastier berries. A statisticalist wants to say that the plant with tastier berries has a higher statistical fitness due to the situation the plants lived in and not caused by the berries being tastier.

However, note that the statisticalist still has to identify the mistletoe with tastier berries, as compared to the mistletoe without the tasty berries, in determining fitness. But how did the statisticalist identify the mistletoe berries, or any other part of the mistletoe's life or reproductive cycle in order to determine the fitness? Life and reproduction are causal interpretations of biology. They are not statistical or physical terms. Physics does not inherently involve biological reproduction or life. To just describe the situation, the greater biological ontology must already be presupposed. Hence the statistical position depends on the causal biological concepts and cannot exist independently of them.

Therefore there is no causal theory of fitness without already having a statistical understanding and there is no statistical theory of fitness without a prior causal understanding. The two theories are mutually dependent, as both are essential to each other and our understanding of them. Specifically, being mutually dependent means that fitness cannot be explained by one, the other, or a mere combination of both causal and statistical theory in a mixed explanation (Ylikoski, 2013). Hence even if we were prepared to accept a dualist position, it wouldn't apply to this situation.

2.3 The Equality of Statistical and Causal Fitness

Given that neither theory is fundamental or distinct, they cannot be used to explain fitness. To explain fitness we would need a more fundamental, well understood theory than the phenomenon in question, which we do not have. Still, fitness is currently described in terms of the interconnected causal and statistical theories and we don't want to lose our understanding of fitness even if there are problems with those theories. So, instead of explaining fitness causally or statistically, what can be done is to interpret fitness causally or interpret fitness statistically. The suggestion is that the causal and statistical methods are the ways fitness is phenomenologically interpreted, not explained, to then understand evolutionary

phenomena.

Though there is no definition of fitness yet — that will come that later — we can now state an equality law describing a basic property of fitness and how we interpret it:

Law of the Equality of Statistical and Causal Fitness: *there is only one kind of fitness and it is our perspective that changes.*

This means that we have the freedom to choose between the causal or statistical method of analysis as the need arises.

One important aspect of the law is that it makes clear that we are not independent, objective observers when it comes to determining fitness. It is our phenomenological perspective that determines which analysis we favor and not something more fundamental about either position. By placing us in-between the statisticalist and causalist positions, it allows us, as an active observer, to bridge the gap between the causal-biological and statistical-physical explanatory schemes.

Secondly, the lack of an absolute perspective demonstrates an important consequence about our epistemic relationship to biological fitness. Though we are not independent observers of fitness, we are all non-independent observers in the same way. Since everyone draws on both accounts, even if only implicitly, we all have the same epistemic foundation for our understanding of fitness.

Lastly note that the equality law explains the qualitative correspondence between the results of the different fitness theories: each is describing the same property, but from a different phenomenological perspective.

2.4 Struggle and Fitness

To further develop this account of fitness, some historical insight is helpful. (Bowler, 1976, 632) identified two different types of biological struggle that existed in Darwin's writings, calling them struggle (a) and (b):

- (a) "This is the real core of the idea of a struggle for existence; for natural selection to work at all, those individuals with favorable variations must compete with and supplant those which are not so favored."
- (b) "... this emerges as the struggle against challenges imposed by the changing nature and limited supply of the other species which serve as food."

As you can see, Bowler's (a) and (b), and indeed Darwin, foreshadow the contemporary distinction between causal and statistical theories. Note, though, Darwin's theories were developed in terms of struggle, not fitness.

This suggests a mapping: let us define a struggle corresponding to each fitness. We can view the struggles for life as either an environmental struggle or

causal struggle. Since these struggles are based on the fitnesses, the difference between environmental and causal struggle is also a matter of perspective. Biological fitness determines how much, how difficult, that struggle is for an organism or population: the fitness is a measure of an organism's or population's *resistance* to struggles.

3 Formalizing Evolution

3.1 Restricted Biological Relativity

With this relation between the struggle for life and fitness we will have the beginning of a new theory of evolutionary biology. To build this theory I'll start by postulating some scientific principles which will lead to a formal foundation for the evolutionary theory. The theory will be universal in the sense that the same concepts of struggle and fitness apply without variation in different places and times, and across different species and environments.

It is not obvious that this is likely or possible. Some species or environments may be better for studying evolutionary struggle than other species or environments. This is to claim that different evolutionary standards could apply to certain species or in different environments. Certain biological formalisms would apply

at one time, and then not at others, making a universality impossible.

For example, note that many, if not all, current theories of evolution include drift (Plutynski, 2007; Rosenberg and Bouchard, 2010). Evolutionary drift is often defined in terms of changes, e.g. changes in gene frequency, in a population not due to Natural Selection. Hence the inclusion of this kind of drift in evolutionary theory indicates that the struggle for life, with respect to Natural Selection, cannot apply universally.

Given this consideration, we can provisionally specify environments in which organisms and populations follow a prescribed struggle for life. Let's start with a controlled environment, one in which we determine who struggles and who doesn't. This is selective breeding and is an instance of human selection. As Darwin noted (Darwin, 1964, 61) there is nothing unique to human selection in that the exact same controlled conditions could have arisen without us in nature. Hence we can treat these cases, ones that are naturally occurring and act as if they were a controlled environment, in the same way as human controlled environments.

Being under control means acting regularly, that is, according to some fixed, formalizable, scheme. Either the situation is stable, or changing in a regular way. Hence, for any such environment, that environment must too be acting relative to some formalizable rules. We can therefore state this as a principle:

Restricted Principle of Biological Relativity: *the same laws of evolution will apply across ecosystems that are uniformly changing.*

The reason that this principle is restricted is that it is limited to ecosystems that are stable or changing in a regular way. Tutt's classic example of the peppered moths during the British Industrial Revolution illustrates this well: the environment was stable except for the single changing factor of sort that directly affected the light and dark colored moths' camouflage (Tutt, 1896, 307). Over 50 years the light colored moths became much less prevalent as compared to the dark moths, since they were now less camouflaged in the darkened environment.

If we consider an ecosystem that is changing in a non-regular way, such as with the introduction of a new competitor, then we will not be able to formalize the system under the Restricted Principle. We will have to wait and see the competitor's effect, if any, and observe if the ecosystem has reacted in a regular way. If it has, then this new ecosystem would fall under the Restricted Principle. Hence the transition from one stable environment to another is outside the scope of the Restricted Principle of Biological Relativity.

3.2 The General Principle of Biological Relativity

We can extend the Restricted Principle of Relativity to its limit by imagining a combination of all the stable and regularly changing environments together. Any formalism that applied across this group would be a fundamental evolutionary theory relative to the uniformly changing environments. If there was a way to include irregularly changing environments along with the regularly changing ones, then we would have the basis for a general theory of biology.

The Law of the Equality of Statistical and Causal Fitness allows us to do just this.

Recall that the Equality Law implies that statistical struggle and competitive struggle yield the same effect on fitness. This means we may account for changes in the environment as if those changes were due to a new competitor, or, conversely, we may account for a new competitor as a statistical environmental change. So no matter what changes occur, there is a formalization scheme. Hence we can explain the transition from a regularly changing environment to an apparent irregularly changing one, and back, by switching interpretive schemes as needed.

Considering the famous moths again, we can imagine a time before the industrial revolution. At that point, the soot on the trees would have been a new

environmental factor that caused an irregular statistical change in what was the prior, uniform environment. However, if we imagine how the moths would have fared if the birds merely preferred to eat light colored moths from the start, and were good at catching them regardless of the soot, then we would arrive at a similar situation. We can treat these two cases, the one with the environmental change and the one where the birds just are better at catching light moths, as equivalent under the Equality Law. Therefore, since the birds' uniform preference is formalizable under the restricted principle, so too must the changing of pre-industrial to industrial environment be formalizable as well.

Therefore taking the Law of the Equality of Statistical and Causal Fitness together with the Restricted Principle of Biological Relativity allow us to extend our formalism to all environments. This gives us the General Principle of Biological Relativity:

General Principle of Biological Relativity: *All ecologies are essentially equivalent for the formulation of the general laws of biology.*

Given new conceptions of fitness, struggle and Natural Selection that satisfy the Equality of Statistical and Causal Fitness and the General Principle of Biological Relativity, we will have a basis for a general evolutionary theory.

To begin, notice that the above relationship between fitness and struggle is

abstract in that fitness is defined as a resistance to struggle. Hence there is no reliance on any particular biological phenomena, such as reproduction or death. A theory that makes use of such a relation between fitness and struggle will be independent of any contingent evolutionary history. The next step is to develop a theoretic implementation that satisfies these conditions.

4 Relativistic Biology

The reader will likely have noticed my regular use of “relativity.” I have done this to highlight the similarity between the biological evolutionary theory presented here and physical relativity theory.

Recall that Einstein developed General Relativity by unifying the two different concepts of mass — inertial and gravitational — that existed at the time. Though inertial mass always equalled the gravitational mass, and vice versa, there was no formal physical relation between the two. Both kinds of mass were needed, but at different times for different experiments. Einstein’s “law of the equality of inertial and gravitational mass,” (Einstein, 1961, 77) declared that there was only one kind of mass, though they were distinguished by our perspective on the situation. This perspective based relativity is described in the famous ‘Space Elevator’ thought

experiment. The above, “Law of the Equality of Statistical and Causal Fitness,” was modeled after Einstein’s Equality Law.

Also note the above General Principle of Biological Relativity,

all ecologies are essentially equivalent for the formulation of the general laws of biology

and Einstein’s (Einstein, 1961, 108):

The following statement corresponds to the fundamental idea of the general principle of relativity: “All Gaussian co-ordinate systems are essentially equivalent for the formulation of the general laws of nature.”

Einstein argued for his General Principle of Relativity by combining his equality law with the accepted notion of classical relativity, which he represented with his Restricted Principle of Relativity (Einstein, 1961, 16). Likewise, the General Principle of Biological Relativity was developed by combining the equality law with an accepted notion, represented by the Restricted Principle of Biological Relativity.

I wish to use this comparison to motivate a new relation between fitness, struggle and Natural Selection as similar to physical mass, acceleration and force. The

new relationship will enable the theory below to have immediate theoretical and practical results.

4.1 *Natural Selection = fitness × struggle*

The relationship between mass, acceleration and force can be described: $F = ma$. Acceleration is the change in velocity over time. Mass is the resistance to acceleration. Force is what causes a mass to accelerate.

Following this example we then define fitness as resistance to struggle, and Natural Selection as: $Natural\ Selection = fitness \times struggle$.¹ Now the task is to biologically interpret this equation such that it satisfies the above General Principle and Equality Law. With these new definitions we will be able to apply the relativistic concepts to evolutionary phenomena and recover scientific results, which is the subject of Section 5 below.

4.2 Struggle, Routine and Acceleration

According to the physical equation, $F = ma$, and the biological one, $N = fs$, there should be a correspondence between struggle and acceleration. Note that

¹Though this is Newton's 2nd Law, it can be used under relativity by substituting relativistic mass for inertial mass in $F = ma$.

acceleration is the change in the rate of motion, the velocity. Struggle is then defined as the change in the rate of phenotypic change. As this definition is abstract, an interpretation follows.

A sense of the word “life” from C.S. Lewis helps explain what is meant here. This sense of life consists of the *Routine*, the general ‘way of’ life, of the individual (Lewis, 1960, 274). In terms of people, Lewis gives the examples from Aristotle of the “nomadic, agricultural, the fisher’s, or the huntsman’s” life, as each consists of different routines.

If we apply this sense of routine with respect to evolution, basic difficulties have to do with the everyday tasks that organisms face. Generally this could include the way that individuals gather food, find shelter, avoid predators, etc. For the mistletoe this includes taking water and nutrients from the host tree, doing photosynthesis and producing berries. Notice that this sort of difficulty is not strictly Tennyson’s “nature red in tooth and claw.” It works just as well being selfish (Dawkins, 2006) as being genial (Roughgarden, 2009). Also important is that reproducing with a degree of variation ought to be included as a routine of a population.

We can also view the routine, everyday tasks as the difficulties that the individual has already evolved to resist. The mistletoe depends upon water and nutrients,

and has satisfied this dependency by evolving a way to acquire these requirements through parasitism on trees.

It is not this sense of daily difficulty, the routine of the individual, in the equation $N = fs$. The struggle, s , indicates a *change in this routine* of an individual's or population's daily life. Struggle is something over and above the everyday difficulties in the routines of the individual or population. When a new Natural Selective force, e.g. a new competitor, is introduced, this changes the routines of a population. This change in everyday life will force the population to either adapt or die off. In this way we have a evolutionary biological interpretation of the abstract mathematical variable s in $N = fs$.

4.3 Fitness, Resistance and Mass

Mass can be understood as how much resistance an object has to acceleration, change in the rate of motion. Analogously, fitness is the resistance to change in the rate of phenotypic change. Perhaps a clearer way of interpreting this is: Fitness can be understood as how much resistance a population or individual has to struggles. The higher a population's fitness, the less it changes its routine; fewer things cause it to struggle, be them perceived as competitors or statistical environmental changes. Another way to interpret this is that fitness is resistance

to change in the rate of adaptation, though ‘rate of phenotypic change’ is the fundamental concept.

To further explain the meaning of routine and fitness, it can be compared to the Red Queen Hypothesis (Valen, 1973). The Red Queen Hypothesis states that populations must be continually evolving in order to just keep their place in their ecosystem. If they were to stop, they would quickly fall behind populations that did keep evolving. Routine can be considered all the things the population does just to keep up with its compatriots and competitors in that ecosystem. The population, say of moths, must continually find food and shelter, avoid predators, resist disease, and produce offspring with heredity and variation. The population’s fitness would be a measure of how consistently it maintains these routines and not fall behind the others in the system.

This description of fitness can also be described as inertial. A population’s fitness determines how well it is able to do whatever it was doing, unless acted upon by some new force, some new struggle that changes its routines.

Gillespie (1977) provides an interesting case because it demonstrates the non-interpreted definition of fitness, fitness as a resistance. He showed that fitness decreases as variance in the offspring number increases. We can view a consistent offspring rate as one method of maintaining the rate of phenotypic change, if all

else is equal. So, under stable conditions, it follows that increasing the variance of the offspring rate will cause the phenotypic rate of change to fluctuate correspondingly. Therefore Gillespie provided an instance of relativistic fitness: he showed, by way of variance in offspring number, that if a population can resist a change in the phenotypic rate of change, the population resists a drop in fitness.

Note that fitness, like mass, can apply to individuals, a population of similar individuals or even an ensemble of dissimilar individuals. Biological relativity makes no claim about the ontological priority of individuals or groups. Depending upon the discussion, groups, individuals or both may be relevant. For example, in discussing altruism one might want to talk about the fitness of a similar group, whereas in discussing clonal organisms the individual could take priority, and when discussing symbiotic relations groups of dissimilar organisms could take priority. This inclusiveness is a benefit considering the diversity of life (Bouchard, 2011).

4.4 Natural Selection, Environment and Gravity

The force of Natural Selection is like the force of gravity according to Einstein's General Relativity. Under General Relativity gravitational force is due to the changing shape of space-time: mass experiences acceleration due to the shape

of space-time at that location and mass also changes space-time at its location. Likewise, a population experiences different struggles due to a changing environment and competition at that location, and, in turn, the population changes the environment and competition as well.

The change that a mass creates in space-time is called its gravitational field. Following this terminology, I'll refer to the overall challenges that a population or individual faces, or creates, at some point in an environment² as the Natural Selection field. This field can therefore be considered aetheric, since it is pervasive, has properties that affect populations and is the fundamental underlying structure of Natural Selection.

An individual or population creates its own Natural Selection field—changing the local environment and competition—by living its life, i.e. performing the routines that make up its daily existence. Conversely an individual or population has to struggle against, exploit or work with the routines of other individuals and populations, as well as environmental routines and patterns. Populations both struggle against and work with the Natural Selection field that is created by them and their environment and, in turn, change the Natural Selection field. It is equal and oppo-

²Just as in Special Relativity, where not space, but space-time, is the fundamental concept, eventually 'environment' will have to be similarly reconceived.

site. In this way Natural Selection mutually affects populations and is changed by those populations in its environment. This account follows Abrams (2007, 2009) in that the fitness of the population cannot be separated from the local environment, and (Glennan, 2005, 338) in that “without the activities and interactions of these individual organisms, there are no changes”.

The change that the Natural Selection field creates can be thought of as a pseudo-force, like relativistic gravity, since it is based upon the irreducible environmental-competitive field, and hence this field provides the causal basis for evolutionary change.

Note that the theory outlined here does not specify any particular biological model or system. It treats all ecologies as equivalent for the study of biological evolution, as is required by the General Principle above in Section 3.2. It also uses a concept of fitness compatible with the Equality Law in Section 2.3. Hence this theory of General Relativistic Biology can act as a law of evolutionary biology.

Insofar as $F = ma$ does not specify a model of the solar system, $N = fs$ similarly has to be developed beyond these abstract grounds to be of practical use. The rest of this essay, therefore, will be dedicated to showing applications of the relativistic approach.

5 Applying Relativistic Biology

With the new definition of struggle, fitness and Natural Selection, we have an evolutionary formalism given by the equation $N = fs$. Gone are reference to survival rates or reproduction, and hence cornerstones of evolution, such as the Survival of the Fittest, cannot remain in their traditional forms under the relativistic view. However, like relativity in physics, nearly all classical results will obtain in relativistic biology under normal circumstances, plus traditionally difficult edge cases become much more manageable under the new concepts.

To start off thinking in terms of relativistic biology, consider what Darwin referred to as ‘living fossils.’ Living fossils, such as the coelacanth or the ginkgo plant, have basically remained unchanged for tens, if not hundreds of millions of years. Their only phenotypic change amounts to trivial rearrangement of their genetics and they have weathered countless competitors and environments. These different competitors and environments — including the genetic environment causing drift — have not caused a change in the routines of the coelacanth or ginkgo plant; they have not caused them to struggle and hence the coelacanth and ginkgo have high fitness. In this way persistence, similar to Bouchard (2008, 2011), is a reflection of high fitness.

A different case is that of humans. The recent global success of humans has

shown we can survive in, and resist the difficulties presented by, many different environments and therefore have a high fitness. Humans are a different case than the living fossils because we demonstrate that persistence is not a critical factor; our species hasn't existed in its modern form for more than a few million years, at most. Whereas we infer the coelacanth has somehow withstood the environmental changes that have happened over the course of history, we withstand many modern environments and competitors.

Now let's return to Tutt's famous moths. The Dark Moths did not struggle during the environmental change of the British Industrial Revolution whereas the Light Moths did. Appealing to $N = fs$ allows us to make a relative judgement of the fitness of the two populations. Since the environmental change was the same, N is constant, say 1 for the sake of the argument. The Light Moths struggled more than the Dark Moths did, so in that environment s_{Light} is *Big* and s_{Dark} is *Small*. Therefore the fitness of the Light Moths is $1/Big$, which is lower than the fitness of the Dark Moths, $1/Small$.

If we imagine that a subpopulation of the Light Moths were able to adapt fast enough to avoid annihilation, perhaps turning into Gray Moths, then these Gray Moths would have a fitness in between the Light and Dark. The Dark moths were able to resist the struggles, meaning they had the highest fitness. The unadapting

Light Moths were unable to resist the struggles, eventually leading to their dying off. The adapting Light Moths, the future Gray Moths, were able to resist more of the struggles by rapidly changing their phenotype. This rapid adaptation—changing the rate of adaptation—allowed the Gray Moths to resist the struggle the environmental change posed better than the Light Moths, but not shake it off as easily of the Dark Moths, meaning that the fitness of the Gray Moths is in between that of the Light and Dark.

Another way to measure Natural Selection, and fitness derivatively, is to see how much force is needed to oppose it. To formalize this, we can take inspiration from Hooke's Law in physics. Hooke's law, $F = -kx$, states we can measure a force (F) acting on a mass by connecting the mass to a spring and suspending in the direction opposing the force (e.g. a supermarket basket scale). By knowing how rigid the spring is (k) and measuring how far the spring has stretched (x) when the connected mass is lifted, we can determine the force acting on the mass: the farther the spring has stretched, the greater the force acting on the object, and the greater the mass of the object.

Similarly we can estimate the Natural Selection on a population by opposing this force: if a population is going extinct, the amount of work we have to do to save it should be equal to the force against it. If a population is doing very

well for itself, say some virus, then the amount of effort it takes for us to contain the outbreak indicates the Natural Selection we are acting against. This gives us, $N = -k_b x_b$ such that k_b is the sophistication of our method used to counteract Natural Selection and x_b is how widespread we've had to employ that method to complete the task.

Consider tuberculosis, which is caused by a bacterial population that we have had some success containing. We've dedicated many political and biomedical resources to its containment, e.g. developing tests for TB and regulating testing for populations like university students in the United States. This means k_b is very high since these are highly sophisticated coordinated efforts. We have also been doing this for a long time and across many universities, meaning x_b is also large. This implies that the force of Natural Selection was high and, derivatively, tuberculosis bacterium has a high fitness. If we now consider that some strains have begun to resist our attempts to contain them, as witnessed by the drug resistant forms of the disease, we can conclude that these strains are even fitter than the previous ones because we will have to expend even more resources to resist them.

5.1 Cornerstones

5.1.1 The Survival of the Fittest

The fittest, according to Relativistic Biology, are the most resistant to struggle, or, resistant to changes in the rate of phenotypic change. Hence there is no specific reliance on reproduction rates.

However, this does not mean the end of the Survival of the Fittest. Consider two populations of very similar organisms with the only difference being one population has many individuals and the other has very few. The small population may even be a tiny subset of the large population. Now consider the large population's resistance to struggle: for any significant change in its routines to occur, it must happen across many individuals. Since the population is large, this change would take a long time and consistent environmental or competitive challenge—a large force—to affect the population.

Now consider the small population. Since that population is small, any change in a few of the individuals will be enough to change that overall population. Hence it will not take much time nor significant environmental or competitive struggle to change this population.

This example shows that more numerous populations are more inherently re-

sistant to struggles than a less numerous population of similar phenotype, by way of the law of large numbers. If everything else is equal, e.g. enough living space and food, it follows that increasing the population increases resistance to struggle. Likewise, decreasing the population decreases resistance to struggle. Hence the Survival of the Fittest survives under relativity insofar as those who do not survive, those who decrease in number, will decrease in fitness, the resistance to struggle.

Classical survival and reproductive rate based fitness theories are then vindicated, in part, since increases in population can indicate increases in resistance to change in the rate of phenotypic change. However, reproduction is now no longer the fundamental metric of fitness but one method of increasing it.

5.1.2 Drift

As mentioned above, many theories of evolution include drift (Plutynski, 2007; Beatty, 1984; Mills and Beatty, 1979; Millstein, 2002; Millstein et al., 2009; Walsh, 2007, 2010; Matthen, 2010). Darwin said in the *Origin* (Darwin, 1964, 81), “Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element...” Generally drift can then be thought of as alternative way that populations can change separate from Natural

Selection. However, drift is part of fitness in relativistic biology and hence not separate from Natural Selection.

To understand this, recall the fundamental uninterpreted definition of fitness: Fitness is a property that indicates resistance to change in the rate of phenotypic change. Hence it is presupposed in the definition of fitness that there is some rate of phenotypic change; natural selection is only recognized with changes of resistance to changes in this rate.

Having a non-zero rate of change should therefore be seen as an adaptive trait of a population. Except for living fossils, which have an extremely high fitness to begin with, a population that has no new adaptations will soon lose out to one that does adapt, and hence a certain degree of variability is necessary in order to generate potential new adaptations. The degree of variability is a critical factor to a population: too little variability and the population will become susceptible to faster adapting competition, and too much variability will yield an unstable, splintered population. Hence sources of variability, such as drift, play an essential role in a population's resistance to struggle, and are not some alternative to Natural Selection.

From the relativistic perspective all changes can be seen as the result of Natural Selection, given the right frame of reference. Contrary to Millstein (2009),

being able to select the ‘relevant level’ at will (see Section 5.2.3 below) does dissolve the distinction between selection and drift, but is not problematic. Imagine there is some change in a human population that could be considered an example of drift, such as a rise in blue eye color. While eye color has no effect on the rate of phenotypic change of humans, if we look at the gene level, the situation is different. According to gene-level accounts (Dawkins, 2006; Sterelny and Kitcher, 1988; Gardner and Welch, 2011), the gene for blue eyes has increased in replication and hence has an increased fitness. Likewise, the relativistic account would view the increased number of genes for blue eyes as an increase in their (the population of genes for blue eyes) resistance to change, as described in Section 5.1.1 above. Hence what looks like an unimportant change at the human level is relevant at the gene level. This result is general to the relativistic position: all biological change is due to Natural Selection on some level or another. As the example shows, though, explaining Natural Selection is a matter of carefully understanding which population is relevant to the change.

Therefore, although there is no longer drift as traditionally conceived, it remains as a fundamental source of variability critical to fitness.³

³There will also be a limit on the precision of the measurement and difficulties in making observations—both an uncertainty principle and ‘special’ relativistic concerns—which also need to be taken into account. These are cases that I hope to return to in the future.

5.2 Non-Darwinian Inheritance

There has been a growing literature of non-Darwinian evolutionary factors that some consider a challenge to contemporary evolutionary theory (Jablonka and Lamb, 2005; Pigliucci et al., 2010; Laland et al., 2013, 2014). Though discussing Darwinian edge-case phenomena in detail is well beyond the scope here, General Relativistic Biology has theoretic resources to straight-forwardly understand and explain non-(straight-forwardly)-Darwinian biological inheritance. Far from presenting difficulties, these Darwinian edge cases provide paradigmatic examples of the benefits of the relativistic approach.

5.2.1 Lamarckism and Epigenetics

A new issue of biological inheritance has been recognized by the recent study of epigenetics. Epigenetics has shown that certain genetic changes, but not to the DNA sequence, acquired during the life of an individual can be passed on to offspring. This is independent of traditional Darwinian inheritance which treats the hereditary material as separate from the environmental situation of an individual and does not address how an organism lived, other than its reproductive rates. Inheritance due to epigenetic changes have been referred to as a new Lamarckism (Jablonka and Lamb, 1995, 2005) harkening back to Lamarck's pre-Darwinian

theory of biological change.

Explaining the fitness benefit of epigenetic change under relativity is straightforward. Epigenetics allow for one phenotype to have different states by regulating gene activity. If one state is better in a certain environment — it allows for greater resistance to struggle — and this is passed along to offspring, then the benefit is passed along. Later, if the situation changes, the organisms are able to morph into a new state. Since both states were already part of the one phenotype, all struggles were resisted by that phenotype.

If we compare this situation to a population that does not use epigenetics, one or both of the different environments may have caused that population to struggle. This population would have either 1) increased the rate of adaptation in order to survive at its current level, that is, changed the rate of phenotypic change, decreasing fitness, or 2) died off, at least in part, again decreasing fitness as described in Section 5.1.1 above.

Hence the greater phenotypic plasticity epigenetics provides means fewer new adaptations are needed to survive different struggles, and therefore epigenetics increases a population's fitness.

5.2.2 Niche Construction

Organisms change their environment in ways beneficial to how they live, and these environmental changes are left to their offspring, who, in turn, benefit from these changes. This creates an environmental-population feedback loop called Niche construction (Laland et al., 2013). The niche supports the population's way of life, and the population works to maintain the niche.

Niche construction is considered non-Darwinian because, like epigenetics, the changes are made during the life of the individual and are then passed on to the offspring. Moreover, the niche is a relationship between the population and its environment and, hence, is a different kind of thing than the hereditary material passed on in Darwinian evolution.

As noted above in Section 4.4, the environment and the organisms mutually interact, and in Section 4.2, the routines of life, which include modifying the local environment, are a fundamental part of the relativistic theory. Hence identifying and understanding Niche construction follows from the definitions of the relativistic theory.

5.2.3 Units and Levels of Selection

An artifact of understanding evolution in terms of reproductive rates is that it is necessary to determine the unit that is reproducing and what counts as reproduction (Lloyd, 2012; Okasha, 2006). Without answers to what the fundamental unit is and what counts as reproduction, such as genes (Sterelny and Kitcher, 1988; Dawkins, 2006), individual organisms (Bouchard and Rosenberg, 2004) or populations of organisms (Millstein, 2006; Godfrey-Smith, 2009), identifying cases of evolution as distinct from other kinds of change is difficult. As argued by (Bouchard, 2011, 113) and (Gilbert et al., 2012, 336), identifying specific units is not just difficult, but impossible, and hence a significant departure from the current approach is called for.

For instance, the Quaking Aspen (Grant, 1993; Bouchard, 2011) can produce what appears to be a forest, but instead is really a single huge organism connected underground by runners. Though it can reproduce sexually, often one initial aspen sends out these runners, creating new “trees” and taking up ever more space. While we initially might perceive many organisms, they are all one interconnected plant that can live many thousands of years. Since this one plant expands but does not reproduce in a traditional fashion, determining its Darwinian fitness is difficult.

We could, with Bouchard (2008, 2011), hold a differential persistence view of fitness, e.g. “compare . . . relative fitness in terms of . . . capacity to still be there in x number of years” (Bouchard, 2008, 569). Though long term persistence provides benefits in many cases that don’t fit easily within prior theories, it piggy-backs on the causal account of evolution like the Statisticalists mentioned above. For instance, consider the differential persistence, and hence fitness, of Mount Everest. Since the mountain has persisted for a long time and will likely continue to persist, it must have high fitness. We can make this claim about the mountain’s fitness because differential persistence makes no reference to any biological property, be it the struggle for life, reproduction, or some other biological phenomenon. This implies that the differential persistence view is dependent upon other, prior theories of evolution, similar to the statistical interpretation above: In order to apply the differential persistence view to biological evolution, we must already have known where biological evolution occurs. Therefore, even though differential persistence does often track the results of evolutionary fitness, in widening evolutionary theory to be more inclusive towards the variety of life, differential persistence widens it too far.

The issue of finding specific units or levels is side-stepped by relativity since it does not prioritize reproduction. As noted above in Section 4.3, relativistic

biology is concerned with any individual or group that resists changes to its phenotypic rate of change. Moreover, with respect to the fundamental unit or population it acts upon, relativistic biology is fundamentally undetermined. The General Principle of Biological Relativity states that all ecologies are essentially equivalent for the formulation of the general laws of biology, which means no environment or level has priority over another.

Returning to the Quaking Aspen, we can appeal to niche construction as well as a modified argument for reproduction. First, by taking up lots of space and being able to transport nutrients via the underground runners, it can more quickly inhabit space than competition, making a niche efficiently (Bouchard, 2011, 112). Secondly, expanding in space can be seen analogously to expanding in population along the same lines as discussed in Section 5.1.1 above: having a larger spatial footprint makes the Aspen more resistant to any localized problem, just like having more individuals.

Noble (2012) argues that level relativity has already been implemented by systems biologists and integrative physiologists. By first showing both upward and downward causation within heart cell models, he then generalizes to a theory of multi-level feedback. He states, “*a priori*, there is no privileged level of causation in biological systems,” (Noble, 2012, 6) that is, biological causation applies at all

levels.

Hence identifying a base unit and its associated ecology is no longer a fundamental requirement of evolutionary theory; according to the General Principle, it cannot be. Natural Selection may act upon any and all groups comprised of any kind of unit. We may investigate the most relevant unit or level in a particular case of Natural Selection—be it a gene or group of dissimilar individuals—but this is an empirical biological question, not a theoretical problem.

6 Conclusion

The focus of this paper was to provide the philosophical basis for, and show the biological usefulness of, evolutionary relativity, such that the initial philosophical problems motivate the biological theory, and the useful applications of the theory lend plausibility to the underlying concepts. Given the success of this scheme, General Relativistic Biology presents a viable alternative to Darwinian Evolution that yields new insights and theoretic tools, while preserving the core, canonical scientific research program.

References

- Abrams, M. (2007). Fitness and propensity's annulment? *Biology and Philosophy* 22, 115–130.
- Abrams, M. (2009, 2). What determines biological fitness? the problem of the reference environment. *Synthese* 166(1), 21–40.
- Beatty, J. (1984). Chance and natural selection. *Philosophy of Science* 51, 183–211.
- Bouchard, F. (2008, 12). Causal processes, fitness and the differential persistence of lineages. *Philosophy of Science* 75(5), 560–570.
- Bouchard, F. (2011). Darwinism without populations: a more inclusive understanding of the “survival of the fittest”. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* 42(1), 106 – 114.
- Bouchard, F. and A. Rosenberg (2004). Fitness, probability and the principles of natural selection. *The British Journal for the Philosophy of Science* 55(4), 693–712.

- Bowler, P. J. (1976). Malthus, darwin, and the concept of struggle. *Journal of the History of Ideas* 37(4), 631–650.
- Darwin, C. (1964). *On the Origin of Species* (Facsimile of 1st ed., 1859, edited by E. Mayr ed.). Cambridge, Massachusetts: Harvard University Press.
- Dawkins, R. (2006). *The Selfish Gene*. Oxford, UK: Oxford University Press.
- Einstein, A. (1961). *Relativity: The Special and General Theory*. New York, NY: Three Rivers Press.
- Gardner, A. and J. J. Welch (2011). A formal theory of the selfish gene. *Journal of Evolutionary Biology* 24(8), 1801–1813.
- Gilbert, S. F., J. Sapp, and A. I. Tauber (2012). A symbiotic view of life: We have never been individuals. *The Quarterly Review of Biology* 87(4), pp. 325–341.
- Gillespie, J. H. (1977). Natural selection for variances in offspring numbers: a new evolutionary principle. *American Naturalist* 111, 1010–1014.
- Glennan, S. (2005). Productivity, relevance and natural selection. *Biology and Philosophy* 24, 325–339.
- Godfrey-Smith, P. (2009). *Darwinian Populations and Natural Selection*. New York, NY: Oxford University Press.

Grant, M. (1993). The Trembling Giant. *Discover Magazine October edition*.

Accessed 18 August 2011.

Hitchcock, C. and J. Velasco (2014). Evolutionary and newtonian forces.

Ergo 1(2), 39–77.

Jablonka, E. and M. J. Lamb (1995). *Epigenetic Inheritance and Evolution: The*

Lamarckian Case. Oxford: Oxford University Press.

Jablonka, E. and M. J. Lamb (2005). *Evolution in Four Dimensions: Genetic, Epi-*

genetic, Behavioral, and Symbolic Variation in the History of Life. Cambridge,

MA: MIT Press.

Laland, K. N., J. Odling-Smee, W. Hoppitt, and T. Uller (2013). More on how

and why: Cause and effect in biology revisited. *Biology & Philosophy* 28(5),

719–45.

Laland, K. N., T. Uller, M. Feldman, K. Sterelny, G. B. Müller, A. Moczek,

E. Jablonka, J. Odling-Smee, G. A. Wray, H. E. Hoekstra, D. J. Futuyma, R. E.

Lenski, T. F. C. Mackay, D. Schluter, and J. E. Strassmann (2014). Does evolu-

tionary theory need a rethink? *Nature* 514, 161–164.

- Lewis, C. S. (1960). *Studies in Words*. Cambridge, UK: Cambridge University Press.
- Lloyd, E. (2012). Units and levels of selection. In E. N. Zalta (Ed.), *The Stanford Encyclopedia of Philosophy* (Spring 2012 ed.). Metaphysics Research Lab, CSLI, Stanford University.
- Matthen, M. (2010). What is drift? a response to millstein, skipper, and dietrich. *Philosophy and Theory in Biology* 2.
- Matthen, M. and A. Ariew (2002, 2). Two ways of thinking about fitness and natural selection. *The Journal of Philosophy* 99(2), 55–83.
- Mills, S. K. and J. Beatty (1979). The Propensity Interpretation of Fitness. *Philosophy of Science* 46(2), 263–286.
- Millstein, R. L. (2002). Are random drift and natural selection conceptually distinct? *Biology and Philosophy* 17, 33–53. 10.1023/A:1012990800358.
- Millstein, R. L. (2006, 12). Natural selection as a population-level causal process. *The British Journal for the Philosophy of Science* 57(4), 627–653.
- Millstein, R. L. (2009, 7). Populations as individuals. *Biological Theory* 3(4), 267–273.

- Millstein, R. L., R. A. S. Jr, and M. R. Dietrich (2009). (mis)interpreting mathematical models: Drift as a physical process. *Philosophy and Theory in Biology 1*.
- Noble, D. (2012). A theory of biological relativity: no privileged level of causation. *Interface Focus* 2(1), 55–64.
- Northcott, R. (2010). Walsh on causes and evolution. *Philosophy of Science* 77, 457–467.
- Okasha, S. (2006). *Evolution and the Levels of Selection*. New York, NY: Oxford University Press.
- Pigliucci, M., G. B. Müller, et al. (2010). *Evolution, the Extended Synthesis*. Cambridge, MA: MIT Press.
- Plutynski, A. (2007). Drift: A historical and conceptual overview. *Biological Theory* 2, 156–167.
- Ramsey, G. (2013). Can fitness differences be a cause of evolution? *Philosophy and Theory in Biology* 5.
- Rosenberg, A. and F. Bouchard (2010). Fitness. In E. N. Zalta (Ed.), *The Stanford*

- Encyclopedia of Philosophy* (Fall 2010 ed.). Metaphysics Research Lab, CSLI, Stanford University.
- Roughgarden, J. (2009). *The Genial Gene*. Berkeley, CA: University of California Press.
- Stephen, C. (2004). Selection, drift, and the “forces” of evolution. *Philosophy of Science* 71, 550–570.
- Sterelny, K. and P. Kitcher (1988, 7). Return of the gene. *Journal of Philosophy* 85(7), 339–362.
- Tutt, J. W. (1896). *British Moths*. London: Routledge.
- Valen, L. V. (1973). A new evolutionary law. *Evolutionary Theory* 1, 1–30.
- Walsh, D. M. (2007). The pomp of superfluous causes: The interpretation of evolutionary theory. *Philosophy of Science* 74, 281–303.
- Walsh, D. M. (2010, 4). Not a sure thing: Fitness, probability, and causation. *Philosophy of Science* 77(2), 147–171.
- Walsh, D. M., T. Lewens, and A. Ariew (2002). The trials of life: Natural selection and random drift. *Philosophy of Science* 69, 452–473.

Ylikoski, P. (2013). Causal and constitutive explanation compared. *Erkenntnis* 78(2), 277–297.